



Genetic parameters estimates for growth performance traits at harvest in Japanese flounder (*Paralichthys olivaceus*)

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ABSTRACT

Despite Japanese flounder (*Paralichthys olivaceus*) is of importance in aquaculture of Northeast Asia, selective breeding programs for growth performance traits remain limited. The aim of this study was to estimate parameters of growth performance traits in this species. The heritabilities, genetic and phenotypic correlations, and breeding values were estimated for body weight (BW), total length (TL), condition factor (K), and average daily gain (ADG). The genetic analyses were performed on a total number of 186 full-sib families (108 sires and 146 dams, 16,807 individuals with integrated pedigree information) from 4 year-classes based on three mixed animal models with tank and year-class as fixed effects, mean family trait values at tagging as a covariate, and additive genetic effect as a random effect using the restricted maximum likelihood method. For all growth traits the maternal and sire-dam interaction effects in proportion to phenotypic variance were very low (0.00–0.05). The heritability estimates for growth traits ranged from 0.12 to 0.39, which is in a low to moderate level. These results indicated that there is a considerable additive genetic variation in growth traits, and the ongoing selective breeding project will produce considerable genetic improvement in growth traits of Japanese flounder. The genetic and phenotypic correlations among BW, TL and ADG were high and positive (0.87–0.94, $P < .001$). However, the correlations between K and other three traits were low to moderate (–0.10–0.58, $P < .001$). These data indicate that these traits (except K) could be selected and enhanced simultaneously and also imply that direct selection of TL, which is an easily measurable trait, will be more favorable than selection on BW and ADG. The estimated breeding values of parents and individuals and the average family breeding values for 4 traits were obtained. In summary, all the findings in this study will be of significance to optimize the flounder selective breeding program.

Statement of relevance: This paper offers guidelines to select breeding strategy in Japanese flounder.

1. Introduction

Japanese flounder (*Paralichthys olivaceus*) is widely cultured along the coast of Northeast Asia and is an economically important marine aquaculture species in the region, mainly including China, Japan, and Korea (Castaño-Sánchez et al., 2010). With the continuous improvement of farming and artificial propagation techniques in China, indoor intensive aquaculture is emerging into practice, which drives major attention to high yield and disease resistance. To achieve this, in the last decade, the breeding program in Japanese flounder has been implemented in practical aquaculture in China. Traditional breeding methods, such as crossbreeding or hybridization (Chen et al., 2008),

and modern genetic technologies, such as gynogenesis, androgenesis and polyploid breeding (Hou et al., 2016; Wang et al., 2012; Yi et al., 2012; Tian et al., 2011b; Wang et al., 2011), have been widely practiced for genetic improvement in flounder. Moreover, marker assisted selection (e.g. genetic linkage mapping and QTL analysis based on growth traits and resistant traits) has been proved an effective method in flounder (Wang et al., 2016; Cui et al., 2015; Shao et al., 2015; Wang et al., 2014; Niu et al., 2012; Pang et al., 2012; Song et al., 2012; Castaño-Sánchez et al., 2010; Fuji et al., 2006, 2007; Coimbra et al., 2003). Besides, preliminary studies on the growth and disease resistant performance have been investigated based on family selection (Zheng et al., 2016; Sun et al., 2015; Zhang et al., 2014b; Liu et al., 2013; Chen

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et al., 2008; Tian et al., 2009; Xu et al., 2008, 2010). However, the systematic selective breeding programs for this species remain limited.

In aquaculture fishes, the main target of selective breeding programs is to enhance growth performance and reduce rearing cycle duration which will lead to more efficient production and higher benefits (Gjedrem and Baranski, 2009). Therefore, growth is considered as an important trait in fish which is cultured for human consumption. The most estimates of genetic parameters of growth traits mainly focus on body weight (BW), total length (TL) and condition factor (K). In livestock, average daily body weight gain (ADG) is considered an important growth trait because it is easy to record and less affected by individual weight at specific ages (Gholizadeh and Ghafouri-Kesbi, 2017; Gyovai et al., 2012). In fishes, however, it was limited by its smaller newborn size and difficulties in individual tagging. Given this reality, we used average family BW at tagging as initial BW of all individuals in this family for calculating ADG individually (see below).

There are numerous studies on genetic parameter estimations of growth traits in other aquaculture fishes, such as Chinese tongue sole, *Cynoglossus semilaevis* (Liu et al., 2016b), common carp, *Cyprinus carpio* (Hu et al., 2017), Atlantic salmon, *Salmo salar* (Powell et al., 2008), rainbow trout, *Oncorhynchus mykiss* (Janhun et al., 2014), Asian seabass, *Lates calcarifer* (Ye et al., 2017) and Nile tilapia, *Oreochromis niloticus* (Gjerde et al., 2012). However, in Japanese flounder, the research literatures of genetic parameters estimation for growth performance traits based on large number of families are very limited. For designing an efficient and practical selective breeding program in this fish, it is needed to obtain accurate estimations of genetic parameters (i.e., heritabilities of the traits of interest and genetic correlations among them). Furthermore, genetic improvement by selection of superior animals based on their estimated breeding values (EBVs) is essential in flounder production and is required to be considered in breeding programs.

In this paper, we estimated heritabilities and breeding values for BW, TL, K, and ADG, as well as the genetic and phenotypic correlations between different growth traits for Japanese flounder by using three different statistical models. To our knowledge, this is the first study that based on a large-scale family selection (involving 186 families with integrated pedigree information) in Japanese flounder.

2. Materials and methods

2.1. Brood stocks

The parental fish were raised in our breeding station in Haiyang, Shandong Province, China. All the fish were individually tagged with Passive Integrated Transponders (PIT) (Qingdao Starfish Instruments Co., Ltd) before using. The initial generation of brood stocks was from three geographic populations (G0), namely South Korea group (KG), Japanese group (JG) and Chinese disease-resistant group (CRG) (Chen et al., 2008). The G0 was collected in 2005, and reached sexual in 2007. Generation one (G1) was produced by G0 on a random mating procedure. The next generation was produced by previous generation using artificial insemination. Then three generations (G1, G2, and G3) were obtained involving five year-classes (YC) (2007, 2009, 2010, 2012, 2013, and 2014). Note that every generation was formed in different year-classes.

All the sires and dams in each generation were from several nuclear families that with a relative high growth rate or survival rate (Chen et al., 2008; Tian et al., 2009; Xu et al., 2010; Zhang et al., 2014a, 2014b; Sun et al., 2015). More details about brood stocks are shown in Table 1. In total, 269 breeders (117 sires and 152 dams) were used in this study. There were complete pedigree records for the breeding population.

2.2. Production of families and fish rearing

The experimental families were established and raised in our breeding station in Haiyang, Shandong province, China. The parental fish were spawned using artificial insemination procedures to create full-sib families in the year-classes of 2012, 2013, 2014, and 2015.

Due to a consecutive spawning type and a high fecundity of flounder, some dams or sires mated with 2–3 dams or sires. Further, some sires and dams were reused across year-classes to create genetic links. During the late April and early May, mature eggs and sperms were stripped from breeders for insemination. The fertilized eggs were incubated in hatchery cages, about 6 h before hatch, they were transferred to 2.5m³ fiberglass-reinforced plastic tanks for hatching and larvae rearing. Finally, each family was cultured in a separate tank, with a similar rearing environment. The tanks were supplied with filtered and sterilized sea water, with a continuous aeration and flowing water exchange (200% per day). Before 30 days post hatch, the water temperature was controlled at 16–20 °C, after that, before tagging, the temperature was not exceeding 25 °C. Salinity was 28–32‰, and dissolved oxygen was 6–8 mg/L. The larvae feeding method was similar to Kim et al. (2011).

At approximately 90 to 120 days post hatch, 800 fry of each family remained in tanks. For evaluation of individual growth performance of each year class, family tagged fish was conducted in several indoor concrete tanks (5 × 6 × 1.2-m, L × W × H) that were supplied with sea water or mixture of sea water and deep well brine, the flow rate was 5 m³/h. The stocking density was 50 fish/m². The salinity and dissolved oxygen were the same with mentioned above. In the 4 year-classes the temperature fluctuated and was not completely same between different year-classes (Table 2). In total, > 200 full-sib families were produced but 186 full-sib families used in this study due to high mortality before tagging or grow-out period. Table 2 shows more information involved in the experiment. During the grow-out period, the fish were fed with commercial dry pellets twice daily, an amount of 3 to 5% of their average live weight.

2.3. Data collection and traits

Before measuring and tagging, fish were anaesthetized with MS-222 (3-aminobenzoic acid ethyl ester methanesulfonate) to avoid handling stress. Newborn fish cannot be reliably tagged for their small size, and families should be reared in separate tanks in the early growth stage. At the age of 120–150 days, fish from each family were tagged with a visible implant elastomer (VIE) (Qingdao Starfish Instruments Co., Ltd), and at the same time, initial (stocking) growth traits of each family were measured and calculated. At the termination of each trial, fish were identified (by family) from the tag codes, counted, and individually measured.

Fulton's coefficient of condition factor based on BW and TL was calculated according to the following formula (Nash et al., 2006):

$$K = 100(BW)/(TL)^3$$

where BW is in grams (g), and TL is in centimeters (cm). Average daily body weight gain (ADG) was calculated as follows:

$$ADG = (W_1 - W_0)/D$$

where W₁ is the BW at harvest, W₀ is the average initial BW of the family, and D is the duration by days. Pedigree data were derived from the first generation (G₀).

2.4. Statistical model

The following mixed animal model was initially used for the four traits:

$$y = \mu + f + r + e$$

Table 1
Details of brood stocks used in this study.

	Group or year-class (no./generation/nuclear family no.)													
	KG	JG	CRG	YC2007	YC2009	YC2010	YC2012			YC2013	YC2014			
Dam	13/G ₀	3/G ₀	5/G ₀	54/G ₁ /5	19/G ₁ /3	17/G ₂ /7	6/G ₁ /1	9/G ₂ /5	8/G ₂ /5	18/G ₃ /8	1/G ₂ /1	-/-/-	-/-/-	-/-/-
Sire	12/G ₀	4/G ₀	3/G ₀	17/G ₁ /5	17/G ₁ /3	21/G ₂ /7	5/G ₁ /1	1/G ₂ /1	3/G ₂ /2	8/G ₃ /3	17/G ₂ /6	4/G ₃ /2	3/G ₂ /2	2/G ₃ /2

where y was the phenotypic observation for the traits; μ is the overall mean; f is the fixed effects, including tank, year-class, and the covariate for the mean family trait values at tagging (the covariate for ADG is mean family BW at tagging); r is the random effects, including the random additive effect for individuals (a), the maternal effect (d), the paternal effect (s), additive genetic sire-dam interaction effect (sd); e showed the residual effects. In the preliminary analysis, significance of fixed effects was tested using the ASReml-R 3.0 software package (Butler et al., 2009). The preliminary analysis results showed that tank and year-class as a fixed effect and average phenotypic values of the family at tagging as a covariate were highly significant ($P < .001$). The effect of geographic population was not significant, so it was not included in the models. According to the above information, the model can be classified as eight models. Table 3 showed the fixed effects and random effects in different models.

In order to choose the most suitable model for each trait, Akaike's Information Criterion (AIC) (Akaike, 1974) was applied as follows:

$$AIC_i = -2\log(R_i) + 2t_i$$

where $\log(R_i)$ is the maximized log likelihood of model i at convergence, and t_i is the number of variance parameters obtained from each model. AIC was calculated for each model using R package AAFun (Lin, 2015) and the model with the smallest value was chosen as the preferred model. For all analyses, the additive genetic relationship matrix included in the model was constructed based on full pedigree traced back to the G₀ generation.

According to the AIC value for each trait in different models (Supplementary table 1), and Model 2 was found to be the most practicable for BW, Model 3 for TL and ADG, and Model 1 for K. Therefore, the models used in this study were showed as follows:

Model 1 $y_{ij} = \mu + f_i + a_j + e_{ij}$

Model 2 $y_{ijk} = \mu + f_i + a_j + d_k + e_{ijk}$

Model 3 $y_{ijkl} = \mu + f_i + a_j + sd_{kl} + e_{ijkl}$

where all parameters are as described above.

2.5. Genetic analysis

The estimation of pedigree-based heritability, (co)variance components and breeding values were estimated using based on the linear mixed animal models (univariate models) using the REML method and ASReml-R 3.0 software package (Butler et al., 2009). The records were converted into a suitable input format and input into the software to

Table 2
Details of family rearing and tagging information of each year-class.

YC	Sires no.	Dams no.	Full-sib family no.	Fish no.	Tank no.	Average no. of fish per family	Duration	Temperature (°C)	Harvest no.	Survival (%)
2012	28	45	53	12,165	4 ^a	230	587	12-20	3846	31.62
2013	16	23	33	5219	2 ^a	158	297	12-18	1720	32.96
2014	27	36	46	7250	6	158	232	16-20	6023	83.08
2015	36	41	54	9686	5 ^a	179	252	12-20	5218	53.87
Total	108	146	186	34,320					16,807	

^a When stocking the fish were in more tanks, in the grow-out period fish were infected with unknown pathogeny with a high mortality, the survival fish were transferred to fewer tanks.

Table 3
The components of fixed effects and random effects in different models.

Model	Fixed effects	Random effects
1	Year + Tank + Covariate	a
2		$a + d + sd$
3		$a + sd$
4		$a + d$
5		$a + s$
6		$a + s + sd$
7		$a + d + s$
8		$a + d + s + sd$

perform univariate and multivariate analysis on the trait (i.e. BW, TL, K, and ADG). Estimated heritability was calculated as follows:

$$h^2 = \frac{\delta_a^2}{\delta_p^2} = \frac{\delta_a^2}{\delta_a^2 + \delta_e^2}, \text{ for Model 1;}$$

$$h^2 = \frac{\delta_a^2}{\delta_p^2} = \frac{\delta_a^2}{\delta_a^2 + \delta_d^2 + \delta_{sd}^2 + \delta_e^2}, \text{ for Model 2;}$$

$$h^2 = \frac{\delta_a^2}{\delta_p^2} = \frac{\delta_a^2}{\delta_a^2 + \delta_{sd}^2 + \delta_e^2}, \text{ for Model 3;}$$

where δ_a^2 was additive genetic variance, δ_p^2 was the phenotypic variance, δ_d^2 was the maternal genetic variance, δ_{sd}^2 was the genetic sire-dam interaction effect variance, and δ_e^2 was the residual variance.

In order to estimate the phenotypic (r_p) and genetic (r_g) correlations for growth traits, multivariate analyses were carried out with three appropriate models derived from univariate analyses (based on the three models without the covariate respectively). Further, AIC values were calculated for each multivariate model using R package AAFun (Lin, 2015), and we found that multivariate analysis based on Model 1 without the covariate with the smallest AIC value (Supplementary table 2). Hence, Model 1 was used in this study for multivariate analyses. The correlations were calculated as follow (Falconer and Mackay, 1996):

$$r_{P/G(xy)} = \frac{\delta_{P/G(xy)}}{\delta_{P/G(x)}\delta_{P/G(y)}}$$

where $r_{P/G(xy)}$ was the phenotypic and genetic covariance between two traits (x and y), and $\delta_{P/G(x)}$ and $\delta_{P/G(y)}$ were the phenotypic and genetic variance of trait x and y , respectively. The t -test was then used to test the significance level of each estimate from zero.

Breeding values (based on best linear unbiased prediction, BLUP) of parents and individuals were estimated and ranked by using 3 models

Table 4
Descriptive statistics of body weight (BW), total length (TL), condition factor (K) at tagging and harvest, and average daily gain (ADG) at harvest in different year-classes (YC).

YC	Tagging BW		Tagging TL		Tagging K		Harvest BW		Harvest TL		Harvest K		Harvest ADG	
	Mean ± SD	CV	Mean ± SD	CV	Mean ± SD	CV	Mean ± SD	CV	Mean ± SD	CV	Mean ± SD	CV	Mean ± SD	CV
2012	24.91 ± 5.85	0.23	14.40 ± 1.96	0.14	0.87 ± 0.09	0.10	391.10 ± 122.70	0.31	34.00 ± 3.58	0.11	0.96 ± 0.11	0.11	0.62 ± 0.21	0.34
2013	34.37 ± 8.74	0.25	12.62 ± 1.05	0.08	0.88 ± 0.07	0.08	192.30 ± 55.51	0.29	26.47 ± 2.73	0.10	1.01 ± 0.10	0.10	0.53 ± 0.19	0.36
2014	38.17 ± 10.04	0.26	16.17 ± 1.45	0.09	0.89 ± 0.08	0.09	233.15 ± 80.26	0.34	28.60 ± 3.36	0.12	0.96 ± 0.12	0.13	0.84 ± 0.33	0.39
2015	40.81 ± 7.28	0.18	16.63 ± 0.89	0.05	0.88 ± 0.04	0.05	197.26 ± 50.64	0.26	27.09 ± 2.52	0.09	0.98 ± 0.11	0.11	0.62 ± 0.19	0.31

respectively. Mean family predicted breeding values were obtained as $1/2u_s + 1/2u_d$, where u_s and u_d are the estimated breeding values of the sire and the dam of every family, respectively. The Pearson and Spearman correlations of estimated breeding value of each growth trait between different models were calculated using R Version 3.4.1.

3. Results

3.1. Descriptive statistics

Preliminary statistical analyses of data were completed using IBM SPSS Statistics 22.0 package. Descriptive statistics for BW, TL, K, and ADG are shown in Table 4. On the whole, the coefficients of variation (CV) for BW, TL, and K at tagging were relatively lower than at harvest in the 4 year-classes. However, for ADG the CVs showed a higher value (0.31–0.39) in the 4 year-classes, which were similar to the values at harvest (0.26–0.34). Furthermore, there was a small fluctuation for the CVs between year-classes for each trait. Year-class 2012 showed the largest value of BW (391.10 g) and TL (34.00 cm) at harvest mainly due to a longer rearing period, and year-class 2014 showed the largest ADG (0.84 g/d) mainly because the rearing temperature was relative higher (Table 2).

3.2. Heritabilities

Estimated variance components and heritabilities for growth performance traits using different models are shown in Table 5. For all traits, the additive variance (δ_a^2) of BW was highest in the 3 models. The ratio of maternal variance (δ_d^2) and sire-dam interaction effect variance (δ_{sd}^2) to phenotypic variance (δ_p^2) detected in 3 models were very low (Table 7). According to the AIC value for each trait in different models (Supplementary table 1), Model 1 was found to be the most practicable for K, Model 2 for BW, and Model 3 for TL and ADG. Therefore, the accurate heritabilities estimated for BW, TL, K, and ADG were 0.12 ± 0.05 , 0.39 ± 0.06 , 0.17 ± 0.03 , and 0.31 ± 0.05 , respectively, which showed low to medium level based on the following classification: low (0.05–0.15), medium (0.20–0.40), high (0.45–0.60), and very high (> 0.65) (Navarro et al., 2009a).

Table 5
Variance components and heritabilities in different statistical models of growth traits of Japanese flounder.

Trait	Model	δ_a^2	δ_c^2	δ_d^2	δ_{sd}^2	δ_p^2	$h^2 \pm SE$
BW	1	2824.09	4012.17	–	–	6836.26	0.41 ± 0.04
	2 ^a	781.00	5006.99	209.41	288.62	6285.85	0.12 ± 0.05
	3	1417.19	4694.77	–	283.46	6395.42	0.22 ± 0.04
TL	1	6.78	4.33	–	–	11.11	0.61 ± 0.05
	2	2.98	6.20	0.21	0.43	9.82	0.30 ± 0.08
	3 ^a	3.87	5.76	–	0.43	10.06	0.39 ± 0.06
K	1 ^a	0.0023	0.011	–	–	0.0133	0.17 ± 0.03
	2	0.0021	0.011	0	0	0.0131	0.16 ± 0.03
	3	0.0021	0.011	–	0	0.0131	0.16 ± 0.03
ADG	1	0.031	0.036	–	–	0.067	0.46 ± 0.05
	2	0.016	0.043	0.001	0.002	0.062	0.26 ± 0.07
	3 ^a	0.019	0.041	–	0.002	0.062	0.31 ± 0.05

^a Indicates the most appropriate model.

Table 6
Genetic correlations (above diagonal) and phenotypic correlations (below diagonal) among flounder growth traits.

Trait	BW	TL	K	ADG
BW		0.94 ± 0.01*	0.40 ± 0.076*	0.87 ± 0.018*
TL	0.90 ± 0.004*		0.38 ± 0.078*	0.91 ± 0.013*
K	0.21 ± 0.015*	–0.10 ± 0.017*		0.58 ± 0.065*
ADG	0.91 ± 0.004*	0.89 ± 0.004*	0.25 ± 0.015*	

* Significance at 0.001 level.

3.3. Genetic correlations

The estimates of genetic and phenotypic correlations for four traits by the multivariate animal model were shown in Table 6. Correlations were classified as low (0–0.40), medium (0.45–0.55) and high (0.60–1), regardless of the sign (Navarro et al., 2009a). The genetic correlations and phenotypic correlations between BW, TL, and ADG were high and positive, 0.87 to 0.94, 0.89 to 0.91, respectively, which were expected. Whereas, low to moderate positive genetic correlations were estimated between K and other three traits, the values were ranging from 0.38 to 0.58, the corresponding phenotypic correlations were much lower, ranging from –0.10 to 0.25. Deserve to be mentioned, the phenotypic correlation between K and TL was negative (–0.10). Nevertheless, all the correlations were significantly different from zero ($P < .001$).

3.4. Estimated breeding value

The ranges of mean family breeding values from univariate analysis for 4 traits were presented in Supplementary table 3. There were wide ranges for BW in three models, –88.70 to 78.55, –53.52 to 37.33, and –78.26 to 56.55, respectively. However, for other 3 traits the ranges were very narrow. Table 7 shows the estimates of Pearson and Spearman correlation coefficients between different models for four traits. All correlations were found to be very high (> 0.86), indicating similar ranking of animals in the three models.

4. Discussion

4.1. Breeding goal and experimental design

In this study, three geographic populations (i.e. China, Korea, Japan) were used initially. Our breeding goal was to obtain hybrids which were offspring of three countries' ancestry. In the 3 statistic

Table 7
The Spearman rank correlation coefficients (below diagonal) and Pearson rank correlation coefficients (above diagonal) of estimated breeding values between different models for growth traits.

Trait model	BW			TL			K			ADG		
	1	2	3	1	2	3	1	2	3	1	2	3
1	1	0.87	0.95	1	0.93	0.96	1	1	1	1	0.96	0.97
2	0.86	1	0.97	0.93	1	0.99	1	1	1	0.95	1	1
3	0.89	0.97	1	0.97	0.99	1	1	1	1	0.97	1	1

models the effect of geographic population was negligible, it was omitted in the later analysis. In Japanese flounder, females matured later than males (females usually 3 years, male 2 years). In order to accelerate breeding process, males were used to produce families earlier, so in our research, every generation was formed in different year-classes. In this case, if genetic parameters were estimated for each generation, the results will be biased, because the rearing conditions (water temperature) and the duration of experiments varied in different year-classes. Though we estimated genetic parameters for mixed generations, we added year-class as a fixed effect to ensure the accuracy of the results.

4.2. Genetic analysis

Three linear mixed animal models were used in this study for genetic analysis. The heritabilities of growth performance traits varies among different models, which could ascribe to different random terms. As the random terms added, the corresponding random effect variance will be separated from genetic variance, and at the same time the residual variance will be reformed. For choosing the most appropriate model, AIC values were calculated for each model and the model with the smallest value was chosen as the preferred model.

A limited number of studies have been reported on heritability estimation for growth traits in Japanese flounder. Liu et al. (2011, 2017) estimated the heritabilities for BW and TL at harvest which was 0.13 and 0.26, 0.29 and 0.35, respectively; Liu et al. (2016a, 2016b) revealed that at 450 days age, the heritability of BW was 0.37, but in the later stages (720 and 830 days) it declined to 0.12 and 0.22. These results were close to ours (0.12 and 0.39, respectively). However, in the early growth stages (before 240 days), the heritabilities of BW and length were much larger. Tian et al. (2011a, 2011b) found that at 2, 3 and 8 months age the heritabilities of BW and body length were 0.35–0.49 and 0.36–0.54, respectively; Shikano (2007) showed that at 210 days age the heritability of body length was 0.81 which was very high. In other flatfish species, the heritabilities of BW and TL were also in a low to moderate level, such as Chinese tongue sole *Cynoglossus semilaevis* (0.13 and 0.13, respectively) (Liu et al., 2016a, 2016b), turbot *Scophthalmus maximus* (0.16–0.33 and 0.17–0.24, respectively) (Lyu et al., 2017; Guan et al., 2016; Zhang et al., 2014a, 2014b), common sole *Solea solea* (0.21 and 0.28, respectively) (Blonk et al., 2010). ADG as a heritable growth related trait was also investigated in this study. The heritability of ADG was 0.31 ± 0.05 , which was larger than BW (0.12 ± 0.05) and close to TL (0.39 ± 0.06). Similar result was found in salmonid, the heritability of daily gain was 0.26 ± 0.18 (Quinton et al., 2007). Heritability for K (0.17 ± 0.03), however, was relatively lower than TL and ADG (0.39 and 0.31, respectively) to some extent. Similar conclusions have been reported for gilthead seabream *Sparus auratus* (Navarro et al., 2009a, 2009b), sea bass *Dicentrarchus labrax* (Dupont-Nivet et al., 2008), grass carp *Ctenopharyngodon idella* (Fu et al., 2015), barramundi *Lates calcarifer* (Domingos et al., 2013), and Nile tilapia *Oreochromis niloticus* (Trong et al., 2013). However, in another flatfish, turbot *Scophthalmus maximus* (Guan et al., 2016), the heritability of K at harvest was very low (0.04), which can be explained because turbot have an oval body shape with a shorter length.

In previous study, the genetic/phenotypic correlations estimated between BW and length in Japanese flounder were highly positive (> 0.84) (Liu et al., 2011; Tian et al., 2011a, 2011b), as well as the other flatfish species mentioned above (> 0.71). These results were consistent with ours (> 0.90). Besides, the genetic/phenotypic correlations between ADG and BW/TL were also very high (> 0.87). However, the magnitude of genetic/phenotypic correlations between other growth traits were low (positive or negative), which was close to the results in turbot (Guan et al., 2016).

4.3. Concluding remarks

The low to moderate heritabilities suggest that selection in a properly designed breeding program in Japanese flounder will result in considerable genetic improvement for target trait at harvest. The high positive genetic and phenotypic correlations between two traits of BW, TL and ADG indicated that selection for one trait will result in another positively correlated response. Compared with TL, BW was more variable and highly dependent on rearing conditions. Moreover, from the perspective of labor saving, we suggest that selection for growth traits can be mainly based on TL. More importantly, we suggest that ADG as a heritable trait should be investigated further for guiding future breeding practice. Meanwhile, the genetic and phenotypic correlations between K and other three traits were low and insignificant, more studies need to be carried out to determine whether K can be used more efficient in breeding program in flounder.

Before establishing a breeding program, breeding goal must be defined, the estimates of genetic variance, heritabilities, phenotypic and genetic correlations among traits must be available, as well as the prediction of breeding values (Gjedrem, 2005). In fish breeding programs, family selection is an important component (Gjedrem, 2005), based on this theory, families were ranked using average family estimated breeding values, and not only that, the predicted breeding values of sires and dams were obtained which have been served for our breeding project in Japanese flounder. In our present work, we estimated Pearson and Spearman correlation coefficients for EBVs for the traits between different models which were all close to unity (Table 7).

To our knowledge, in Japanese flounder, this is the first study that heritabilities, genetic and phenotypic correlations, and breeding values were estimated for 4 growth performance traits based on a large dataset (involving 186 families and 16,807 individuals) and complete pedigree information using univariate or multivariate animal mixed model methodology. Finally, according to the results presented in this study, from a genetic improvement perspective the improvement of these traits simultaneously is plausible.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.aquaculture.2018.01.010>.

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